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# Frontal Brain Potentials during Recognition Are Modulated by Requirements to Retrieve Perceptual Detail

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## Summary

**To assess the role of prefrontal cortex in retrieval and address the controversy about whether prefrontal retrieval operations are engaged only following successful retrieval, we recorded event-related brain potentials during two recognition tests with differing demands on retrieval effort. Both tests included object drawings that were (1) identical to those studied, (2) the same but with altered aspect ratios, and (3) previously unseen. Instructions were to respond "old" only if drawings were not modified (specific test) or regardless of modifications (general test). Frontal potentials were enhanced during the specific relative to the general test for all three types of drawings. We conclude that these potentials reflected differential engagement of strategic retrieval, that this function relied on left prefrontal cortex, and that it was not contingent on successful retrieval.**

## Introduction

Historically, descriptions of frontal lobe function have emphasized planning, attention, and working memory (Luria, 1973; Pribram, 1973; Shallice, 1982; Goldman-Rakic, 1987; Knight and Grabowecky, 1995). Recently, however, frontal contributions to long-term memory have received considerable emphasis. Patients with prefrontal lesions do not display the typical amnesic syndrome associated with lesions of the medial temporal lobes or diencephalon, but they do tend to exhibit three types of memory impairment: (1) poor memory for the context in which a memory was acquired (Janowsky et al., 1989; Shimamura et al., 1990; McAndrews and Milner, 1991; Milner et al., 1991; Butters et al., 1994; Mangels, 1997), (2) moderate deficits in free recall (Jetter et al., 1986; Hirst and Volpe, 1988; Incisa della Rochetta and Milner, 1993; Stuss et al., 1994; Gershberg and Shimamura, 1995), and (3) mild impairments on tests of item recognition (Wheeler et al., 1995).

These neuropsychological findings have led to competing hypotheses regarding the role of prefrontal cortex in episodic memory retrieval. One view is that prefrontal cortex controls strategic processing at retrieval, which is often key to a search for information from memory. An alternative view is that prefrontal cortex is selectively engaged following successful retrieval; when a stimulus matches a stored representation, prefrontal cortex is needed to retrieve additional information. This information is then used to reinstate the context of the relevant episode. With the assumption that contextual retrieval is more important for recall than for recognition, the neuropsychological evidence can be accounted for by either of the two hypotheses.

Studies of memory using positron emission tomography (PET) tend to support the hypothesis that prefrontal activity reflects strategic retrieval and is independent of retrieval success. In one experiment, retrieval success was manipulated by comparing a test with a high proportion of old items to a test with a low proportion of old items (Kapur et al., 1995). In another experiment, retrieval success was manipulated by comparing well-remembered words that were encoded semantically to poorly remembered words that were encoded perceptually (Nyberg et al., 1995). In both experiments, right prefrontal activation was found during recognition testing relative to encoding, and the level of activation was insensitive to the amount of successful retrieval. These researchers concluded that activation of right prefrontal cortex is related to the attempt to retrieve information, regardless of the success or failure of the attempt.

However, prefrontal activation was associated with retrieval success in a subsequent PET study (Rugg et al., 1996). This association was based on a comparison between blocks of mostly old items and blocks of only new items, and the authors proposed that this comparison provided greater sensitivity than comparisons between conditions with high versus low proportions of old items. However, some doubt can be cast on this link between prefrontal activity and retrieval success, due to the possibility that these PET findings reflected differences in strategies induced by using blocked stimulus sequences (cf. Johnson et al., 1997). This possibility was supported by recent experiments using functional magnetic resonance imaging (fMRI). In a blocked stimulus presentation design, right prefrontal activation was observed during blocks of well-remembered words relative to blocks of poorly remembered words (Buckner et al., 1998b). When stimulus presentation was randomized and hemodynamic responses to individual trials were examined, right prefrontal activation was equal for correctly recognized old words and correctly rejected new words (Buckner et al., 1998a). The authors concluded that right prefrontal activity may be modulated by shifts in retrieval strategies induced by blocked stimulus presentation, but that it is not contingent upon retrieval success. However, in light of the apparent absence of old–new differences in other parts of the brain, these right prefrontal findings may reflect insufficient statistical power.

Further insight into these issues might be gained through the use of multiple methods to monitor prefrontal activity. Event-related potentials (ERPs), in particular, can readily be recorded with either randomized or blocked stimulus sequences and provide direct measures of neural activity with temporal resolution on the order of milliseconds. Although present methods do not allow for precise localization of neural regions that contribute to scalp-recorded ERPs, their temporal resolution may make it possible to monitor critical events that

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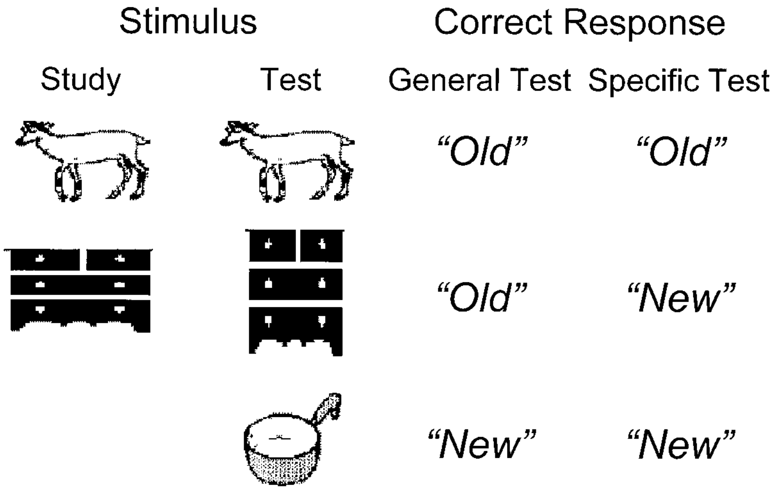

Figure 1. Stimulus Types

Sample pictures illustrate each condition. For old/same pictures (top), the correct response is "old" in both tests. For old/different pictures (middle), the correct response is "old" in the general test and "new" in the specific test. For new pictures (bottom), the correct response is "new" in both tests.

are too brief to elicit a reliable hemodynamic response. Furthermore, ERP and hemodynamic methods may provide complementary sources of evidence regarding the role of prefrontal regions in memory retrieval, due to the fact that the two methods are subject to different limitations and are sensitive to different subsets of neural activity (Roskies, 1994; Posner and Raichle, 1995, and associated commentaries; Kutas and Dale, 1997; Rugg, 1998).

Evidence from one ERP study appears to support the idea that right prefrontal activity is sensitive to retrieval success (Wilding and Rugg, 1996). Participants first heard spoken words. They then read words and made an old/new judgment for each word. For each old word, they also judged whether it had been spoken in a male or female voice at study. An ERP recorded over right frontal scalp locations was enhanced for recognized old words that were attributed to the correct voice. The authors interpreted these findings as evidence that right frontal brain regions were involved in effortful retrieval of perceptually detailed source-specifying information, which is thought to characterize successful episodic memory retrieval (Tulving, 1983; Johnson et al., 1993).

The apparent discrepancy between these right frontal ERP effects (Wilding and Rugg, 1996) and event-related fMRI results showing that right frontal activity did not differ between old and new words (Buckner et al., 1998a) can be interpreted in several ways. First, ERP measures may be more sensitive than hemodynamic measures to right frontal activity associated with retrieval success. Another possibility is that the source recognition test employed by Wilding and Rugg (1996) required more recollection of detailed perceptual information than did the recognition test used by Buckner and colleagues (1998a), and that right frontal activity is associated with retrieval success when detailed recollection is required.

In the present experiment, we sought to clarify these issues by monitoring brain potentials during two recognition tests with identical study and test items but differing retrieval demands. In each test, participants viewed line drawings of objects (Figure 1), one-third of which were identical to those viewed in the study phase (old/same), one-third of which were old pictures with modified aspect ratios (old/different), and one-third of which were new. In the general test, participants were instructed to endorse all studied pictures as old, regardless of whether they had been modified. In the specific test, participants were instructed to endorse identical pictures as old and to endorse modified old pictures and unstudied pictures as new. Because the specific test placed greater demands on effortful retrieval of perceptual detail than did the general test, we were able to assess whether frontal brain activity was sensitive to retrieval effort, as well as whether this activity was contingent upon retrieval success.

## Results

### Behavioral Results

Mean recognition scores and reaction times for correct responses are shown in Table 1. An analysis of variance (ANOVA) for old pictures revealed that recognition was reliably more accurate for old/same than old/different pictures ($F[1,11] = 11.30$, $p < 0.006$). Accuracy was also higher in the general test than in the specific test ($F[1,11] = 71.28$, $p < 0.001$). This difference in accuracy between the two tests was similar for the two types of old pictures ($F[1,11] < 1$) and averaged 17.5%. Accuracy for new pictures did not differ between the general and specific tests ($F[1,11] < 1$).

Reaction time results mirrored those for recognition

Table 1. Recognition Performance as a Function of Stimulus Type and Test Condition

| Measure and Test Condition | Stimulus Type<br>Old/Same | <br>Old/Different | <br>New |
|---|---|---|---|
| Accuracy (% correct) | | | |
| General Test | 96.2 (0.8) | 90.0 (1.9) | 96.0 (1.2) |
| Specific Test | 81.0 (2.2) | 69.9 (4.2) | 96.1 (0.7) |
| Reaction time (ms) | | | |
| General Test | 830 (30) | 899 (58) | 901 (51) |
| Specific Test | 1058 (44) | 1101 (50) | 908 (48) |

SEM in parentheses.

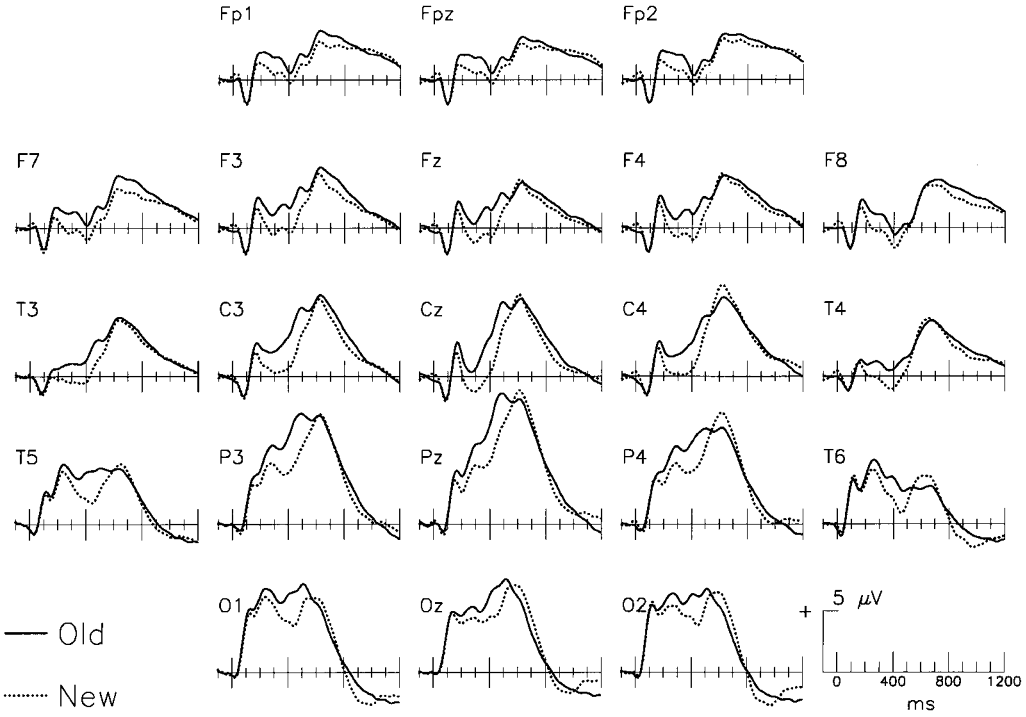

Figure 2. ERPs to Old and New Pictures

ERPs from all scalp locations are arranged topographically, as viewed from above, with frontal locations at top. Solid lines show responses to old pictures; dotted lines show responses to new pictures.

accuracy. Reaction times were significantly faster for old/same than for old/different pictures ($F[1,11] = 7.03$, $p = 0.023$). Responses were also faster in the general test than in the specific test ($F[1,11] = 44.60$, $p < 0.001$). The influence of test condition on reaction time was similar for the two types of old pictures ($F[1,11] < 1$) and averaged 215 ms. Reaction time for new pictures did not differ between the general and specific tests ($F[1,11] < 1$).

### ERP Analysis Strategy

We planned a set of initial ERP comparisons based on results from prior studies. First, we analyzed ERP differences between old and new pictures, as effects of this sort have been observed in prior ERP studies of memory (Paller, 1993; Johnson, Jr., 1995; Rugg, 1995). Given that these effects were often maximal at parietal scalp locations, one analysis focused on midline parietal results. We predicted that the magnitude of the parietal old–new ERP difference would be greater for old/same than for old/different pictures due to their closer correspondence to studied pictures. An additional analysis of right frontal old–new effects was conducted to allow comparisons to be made with prior results linking such effects to episodic recollection (e.g., Wilding and Rugg, 1996, 1997a; Schloerscheidt and Rugg, 1997; Wilding, 1999). The comparisons most closely tied to the rationale for our experiment were between the specific and general test conditions, and we hypothesized that these differences would appear at frontal scalp locations. We sought to determine whether this ERP effect was apparent only for old pictures, as would be predicted if the potentials reflected frontal retrieval operations engaged only after successful retrieval, or for both old and new pictures, as would be predicted if the potentials reflected frontal retrieval operations engaged irrespective of retrieval success.

### ERP Results

Brain potentials to old and new pictures are shown in Figure 2. An enhanced positivity in ERPs to old pictures was apparent from ~200 to 500 ms after stimulus onset, particularly at central and parietal locations. This old–new effect was qualitatively similar for old/same and old/different pictures (Figure 3A). Specifically, at the midline parietal scalp location, mean amplitudes from 300 to 500 ms were more positive for old/same and old/different pictures than for new pictures ($F[1,11] = 42.50$, $p < 0.001$ and $F[1,11] = 16.91$, $p = 0.002$, respectively). Moreover, ERPs from 300 to 500 ms were more positive for old/same than for old/different pictures ($F[1,11] = 6.78$, $p = 0.025$).

The scalp topography of the old–new effect was remarkably similar for the two types of old pictures, as shown in Figure 3B. To verify this impression, an ANOVA was performed on data from all electrode locations using mean amplitudes from 300 to 500 ms, normalized by the vector length method so that the topographic analysis would be independent of amplitude differences (McCarthy and Wood, 1985). The stimulus type by location interaction was not statistically significant ($F[20,220] < 1$), suggesting that the same configuration of intracranial generators was active during this period for old/same and old/different pictures.

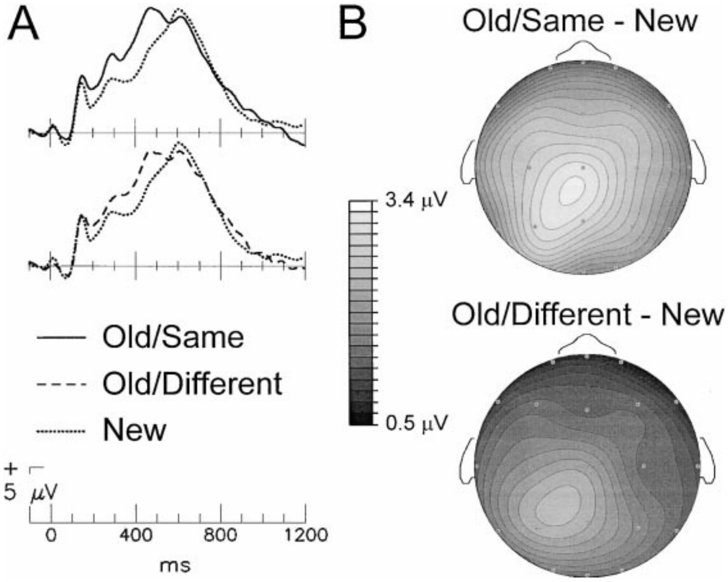

Figure 3. Old–New ERP Effects for Both Types of Old Pictures

(A) Midline parietal ERPs are shown for old/same pictures (solid), old/different pictures (dashed), and new pictures (dotted).

(B) Topographic maps of the old–new ERP differences, computed by a surface spline interpolation, display a centroparietal maximum. Mean amplitude differences were measured from 300 to 500 ms. Each small circle represents an electrode location on a schematic head, as viewed from above.

In addition, a right frontal old–new difference was observed at a longer latency. As shown in Figure 4, this later old–new difference was larger during the general test than during the specific test. To quantify this effect, mean amplitudes were measured from 900 to 1100 ms. At the right lateral frontal location, ERPs to old pictures were significantly more positive than those to new pictures during the general test ($F[1,11] = 7.57$, $p = 0.019$) but not the specific test ($F[1,11] < 1$). The amplitude of the old–new difference in the general test was larger at the right compared to the left lateral frontal location (1.12 µV versus 0.24 µV, respectively), although this hemispheric asymmetry was not statistically significant ($F[1,11] = 3.38$, $p = 0.093$).

ERPs averaged separately for the specific and general tests are shown in Figure 5. We refer to ERP differences between the two test conditions as test effects. Test effects were particularly prominent at anterior scalp locations, where ERPs to pictures presented in the specific test were more positive than ERPs to pictures presented in the general test. In contrast, test effects were minimal at posterior scalp locations. A topographic map of the test effect, measured over the 500–1200 ms interval at each electrode location, clearly demonstrates the left frontal distribution of the effect (Figure 6A).

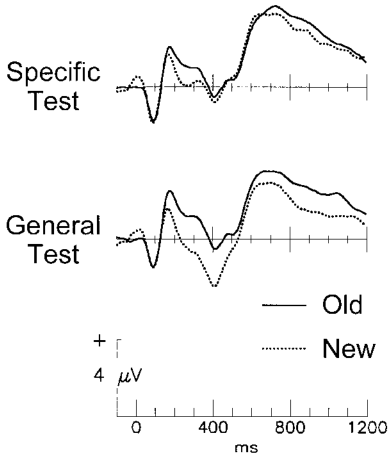

Figure 4. Right Frontal ERPs to Old and New Pictures

ERPs from the right lateral frontal electrode are compared across the specific and general tests for old pictures (solid) and new pictures (dotted).

In one analysis of the test effect, mean ERP amplitude measurements over the 500–1200 ms interval from left and right frontal electrode locations were submitted to an ANOVA with four factors: test (specific, general), stimulus type (old/same, old/different, new), location (anterior frontal, midfrontal, lateral frontal), and hemisphere. ERPs were significantly more positive during the specific test than during the general test ($F[1,11] = 11.15$, $p = 0.007$). In addition, a significant test by hemisphere interaction ($F[1,11] = 6.27$, $p = 0.029$) indicated that the test effect was larger at left than at right frontal locations. The only other significant effect in this analysis was a test by stimulus type by location interaction ($F[4,44] = 3.51$, $p = 0.02$), which reflected the finding that the maximal test effect was recorded at the left lateral frontal location for old/same and new pictures but at the left midfrontal location for old/different pictures. However, analyses on normalized data (see below) are more appropriate for topographic comparisons of this sort.

Given that the amplitude of the overall test effect was maximal at the left lateral frontal location (Figure 6A), additional analyses were conducted on recordings from this scalp location. Specific–general differences were analyzed in consecutive 100 ms epochs from 0 to 1200 ms. Significant differences were found in each epoch from 500 to 1200 ms ($Fs[1,11] > 5.02$, $ps < 0.05$), with marginal trends from 300 to 500 ms ($F[1,11] = 4.43$, $p = 0.059$ and $F[1,11] = 3.62$, $p = 0.084$). These results confirm the appropriateness of the 500–1200 ms interval for analyses of test effects.

Test effects at the left lateral frontal location were also analyzed separately for each stimulus type (Figure 6B).

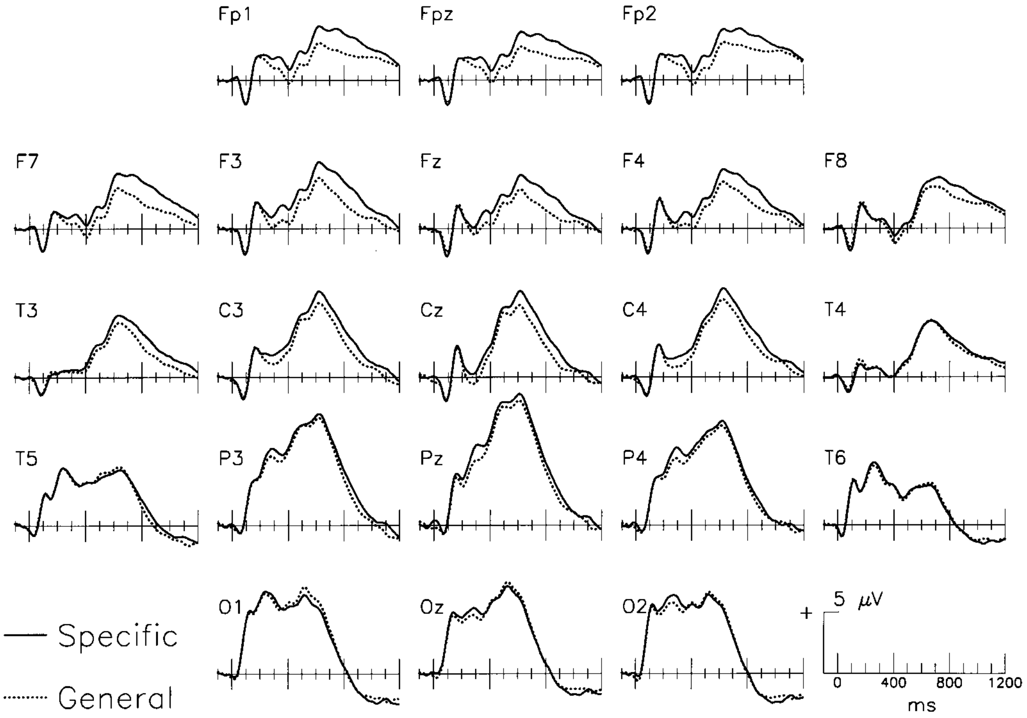

Figure 5. ERPs during Specific and General Tests

ERPs from all scalp locations are arranged topographically, as viewed from above, with frontal locations at top. Solid lines show responses to pictures in the specific test; dotted lines show response to pictures in the general test.

A test by stimulus type ANOVA on mean amplitudes from 500 to 1200 ms showed that ERPs were significantly more positive during the specific test than during the general test (F[1,11] = 16.44, p = 0.002). In addition, a nonsignificant test by stimulus type interaction (F[2,22] < 1) indicated that the magnitude of the test effect did not differ across stimulus type (in accord with the nonsignificant test by stimulus type interaction in the analysis of left and right frontal recordings reported above). In addition, test effects were significant for each stimulus type tested separately (1.1 $\mu$V for old/same, F[1,11] = 5.17, p = 0.044; 1.4 $\mu$V for old/different, F[1,11] = 11.71, p = 0.006; 1.3 $\mu$V for new, F[1,11] = 5.05, p = 0.045). The onset of the test effect appeared to differ across stimulus type, and in analyses for the interval from 300 to 500 ms, only the test effect for new pictures was significant (F[1,11] = 8.51, p = 0.014).

To determine whether the scalp topography of the test effect differed across stimulus type, we conducted additional analyses using mean amplitude differences from 500 to 1200 ms normalized by the vector length method (McCarthy and Wood, 1985). When all 21 electrode locations were included, the stimulus type by location interaction was nonsignificant (F[20,220] < 1). Likewise, when only the 6 left and right frontal electrode locations were included, all interactions involving stimulus type were nonsignificant (stimulus type by location F[4,44] = 1.43, p = 0.26; stimulus type by hemisphere

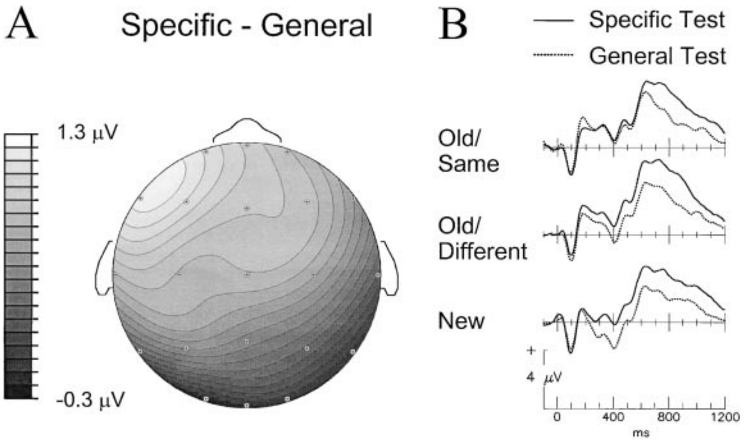

Figure 6. Topography of the Test Effect, with Left Frontal ERPs for Each Stimulus Type

(A) The topographic map of the test effect, computed by a surface spline interpolation, displays a left frontal maximum. Mean amplitude differences were measured from 500 to 1200 ms. Each small circle represents an electrode location on a schematic head, as viewed from above.

(B) ERPs from the left lateral frontal electrode during the specific test (solid) and general test (dotted) for old/same, old/different, and new pictures. Test effects were apparent in the interval from 500 to 1200 ms for each stimulus type.

$F[2,22] = 1.39$, $p = 0.27$; stimulus type by location by hemisphere $F[4,44] < 1$). Thus, frontal ERPs were more positive during the specific test than during the general test for old and new pictures, and the left frontal scalp topography of the test effect did not differ reliably between the three stimulus types.

## Discussion

The purpose of this study was to determine the extent to which frontal lobe activity during memory retrieval is modulated by (1) retrieval success and (2) retrieval effort. Consistent with previous results, we observed old–new ERP effects that may reflect recollective processing. We will discuss these results first and then turn to the finding that frontal brain potentials were modulated by the retrieval demands of the recognition test.

### Parietal Old–New Effects

We observed a larger positive response for old pictures than for new pictures from 200 to 500 ms, maximal at centroparietal scalp regions (Figure 2). The magnitude of this ERP difference was larger for old/same than for old/different pictures (Figure 3), paralleling the faster and more accurate recognition responses for old/same than for old/different pictures (Table 1). ERP repetition effects have been observed with various types of stimuli, including drawings of objects (Kazmerski and Friedman, 1997; Schloersheidt and Rugg, 1997), photographs of faces (Paller et al., 1999), auditory words (Senkfor and Van Petten, 1998), and visual words (reviewed by Paller, 1993; Johnson, Jr., 1995; Rugg, 1995). In some cases, positive ERPs to old items were linked to conscious recollection (e.g., Paller and Kutas, 1992; Smith, 1993; Paller et al., 1995; Wilding and Rugg, 1996; Rugg et al., 1998; Paller et al., 1999).

The contrast between old/same and old/different pictures is an important feature of our experimental design. Old/different pictures were not quite identical to pictures presented during the study phase. The finding that recognition accuracy and the magnitude of the parietal old–new effect were both greater for old/same than for old/different pictures supports the conclusion that old/same pictures elicited memories that were, on average, more perceptually vivid than those elicited by old/different pictures. We further speculate that participants paid special attention to the perceptual vividness of memories during the specific test in order to differentiate old/same from old/different pictures.

### Right Frontal Old–New Effects

Brain potentials elicited by old pictures were also more positive than those elicited by new pictures from 900 to 1100 ms, particularly at the right frontal scalp region. This effect was similar in time course and topography to effects observed in other ERP studies of memory (Wilding and Rugg, 1996, 1997a, 1997b; Allan and Rugg, 1997; Düzel et al., 1997; Schloersheidt and Rugg, 1997; Trott et al., 1997; Donaldson and Rugg, 1998; Mark and Rugg, 1998; Wilding, 1999). In some experiments that reported a right frontal old–new effect, the test procedure required retrieval of specific perceptual information, and the magnitude of the effect was larger when this information was correctly remembered (Wilding and Rugg, 1996, 1997a; Mark and Rugg, 1998; Wilding, 1999). This evidence suggests that right prefrontal cortex plays a role in the retrieval of specific perceptual information.

However, it should be noted that right frontal old–new effects have also been reported in other studies that did not emphasize perceptually detailed retrieval (e.g., Allan and Rugg, 1997; Schloersheidt and Rugg, 1997). Furthermore, in some studies in which retrieval of specific perceptual information was required, right frontal old–new effects were not observed (Wilding et al., 1995; Johnson et al., 1996; Senkfor and Van Petten, 1998). In the present study, a right frontal old–new effect (Figure 4) was apparent when retrieval of detailed perceptual information was not necessary (general test) but not when retrieval of such information was necessary (specific test). Collectively, these findings suggest that right frontal ERPs tend to differ between old and new items, but that this differential response is not specifically associated with the retrieval of detailed perceptual information that characterizes successful episodic recollection.

### Frontal Test Effects

Our primary result was that frontal brain potentials differed systematically between the two test conditions, in that responses in the specific test were more positive than those in the general test. Although the time courses of these effects for old/same, old/different, and new pictures were not identical (Figure 6B), robust test effects were observed for all three stimulus types. One way to account for ERP differences between the specific and general test conditions is to suppose that they were due to the greater difficulty of the specific test and were merely secondary to differences in reaction time and accuracy. However, the pattern of behavioral data casts doubt on this explanation. Accuracy and reaction time varied across the two tests for old pictures but were virtually identical for new pictures, whereas similar frontal test effects were found for old and new pictures. Furthermore, other nonspecific explanations for the test effects can be ruled out because there were no systematic physical stimulus differences across the two tests, due to the counterbalanced design.

One factor that was not controlled between the specific and general tests was response probability. Two-thirds of the items in the general test were called “old,” whereas only one-third of the items in the specific test were called “old.” Nonetheless, the idea that this factor was responsible for ERP test effects is inconsistent with the finding that similar test effects were observed for old and new pictures. If differences in response probability rather than retrieval processing were responsible for ERP differences between the two tests, opposite patterns of test effects would be expected for old and new pictures, because the probabilities of responding “old” and “new” varied inversely between the two test conditions. It is thus unlikely that differences in response probability had a significant influence on left frontal test effects.

We therefore interpret the ERP test effects as a reflection of changes in strategic processing associated with our manipulation of retrieval demands. The focal left frontal topography of this ERP difference (Figure 6A) lends itself to the interpretation that it was produced by differential neuronal activity in left prefrontal cortex. Although our scalp ERP evidence on its own is ambiguous with respect to intracranial electrical sources, the neuropsychological and neuroimaging findings discussed above provide additional evidence to support the hypothesis that left prefrontal cortex is instrumental for strategic retrieval processing. It is therefore reasonable to interpret the ERP test effects as an indication of retrieval processing resulting from left prefrontal activity.

Our results are consistent with previous reports of frontal ERP differences related to the specificity of episodic retrieval demands (Johnson et al., 1996; Senkfor and Van Petten, 1998), but they also suggest that this prefrontal function applies to both old and new items. Thus, our results favor the hypothesis that prefrontal involvement in episodic retrieval is not limited to the retrieval of contextual information, and that at least some prefrontal regions are responsive to changes in retrieval effort. Retrieval effort probably encompasses multiple cognitive processes, and fortunately the design of the present experiment allows us to elaborate further on the specific types of processing implemented by prefrontal cortex in these circumstances.

We suggested above that perceptual vividness was greater for memories elicited by old/same pictures than for memories elicited by old/different pictures. It follows that perceptual vividness would be a useful cue for differentiating old/same from old/different pictures in the specific test. We propose that retrieval effort associated with the ERP test effect may have consisted of at least two factors. First, participants may have allocated more attentional resources to processing specific perceptual attributes of test items during the specific test than during the general test. Second, participants may have also maintained these perceptual details in working memory in order to evaluate a possible match with the results of memory retrieval. In order to make complex memory attributions, as in the specific test, specific features of the recollective experience must be actively maintained and evaluated in working memory, thus demanding prefrontal resources (see Shimamura, 1996, for a similar view). This proposal integrates findings regarding the role of prefrontal cortex in episodic memory with the idea that left prefrontal regions play a critical role in the maintenance and manipulation of information in working memory (Goldman-Rakic, 1987; Fuster, 1989; Cohen and Servan-Schreiber, 1992; Petrides et al., 1993; Cohen et al., 1996; D'Esposito et al., 1999).

In conclusion, our electrophysiological results provide direct support for the idea that prefrontal regions are engaged in strategic processing in response to retrieval demands (Moscovitch, 1989; Shimamura, 1996). These results complement findings from neuroimaging (Kapur et al., 1995; Nyberg et al., 1995; Buckner et al., 1998a) and suggest that this role is not contingent upon conditions of successful retrieval. Left prefrontal cortex, in particular, appears to have contributed to strategic retrieval operations in the specific test.

Speculations about functional differences between the right and left frontal lobes in memory have been the focus of considerable controversy in recent years. Results from neuroimaging and ERP studies suggest that right prefrontal regions may be more active during episodic retrieval tasks than during other types of tasks (Tulving et al., 1994; Buckner, 1996; Nyberg et al., 1996; Ranganath and Paller, 1999). Therefore, it was surprising that ERP differences between the specific and general tests were left lateralized. However, in a recent review of neuroimaging studies of memory, Nolde and colleagues (1998a) suggested that right prefrontal activity is sensitive to whether or not one is engaged in an episodic retrieval task, whereas left prefrontal activity is sensitive to the specificity of episodic retrieval. Moreover, findings from a recent event-related fMRI study directly linked left prefrontal activation with the specificity of recognition testing (Nolde et al., 1998b). Participants in this experiment studied words and pictures and then were scanned during recognition testing with words only. In one test condition, participants made old/new judgments; in another, they had to specify whether each word was studied as a picture, studied as a word, or previously unstudied. Results showed that left prefrontal regions were more active during the specific recognition condition than during the old/new recognition condition, whereas right prefrontal regions were activated equally during the two test conditions. These findings reinforce our conclusion that evaluating the potential match between a recognition cue and retrieved information—a process critical for accurate episodic recollection—relies on neuronal activity in left prefrontal cortex.

## Experimental Procedures

### Participants

Six men and six women from the Northwestern University community were paid for participating in the experiment. They were right handed and ranged in age from 18 to 22 years. Data from four additional participants were discarded (two because of technical difficulties and two because of excessive eye and muscle artifacts).

### Stimuli

Stimuli were derived from 300 pictures of objects used in previous studies of picture memory (Snodgrass and Vanderwort, 1980; Park et al., 1997, Schizophr. Res., abstract). Each picture was manipulated to create a wide version (125% horizontal, 75% vertical scaling) and a long version (75% horizontal, 125% vertical scaling), resulting in a total of 600 pictures (not including the original pictures, which were not used in this study). The average picture size was ~40 mm × ~40 mm.

### Procedure

Each participant was fitted with an electrode cap (see below) and seated in a sound-attenuating chamber. Participants were given task instructions and also instructed to try to relax neck and facial muscles and to avoid blinking or moving while performing the experimental tasks. Stimuli were presented on a video monitor about 140 cm away. Responses were made with two buttons, one for each hand.

The experiment consisted of 20 study test blocks. In each study phase, ten pictures were presented twice (each time in a different random order), followed by one filler picture that was not used in the subsequent test. The exposure duration for each picture during the study phase was 630 ms. The picture was then replaced by a fixation cross. For each picture, participants were instructed to push the right button if the highest point on the right half of the picture was higher than the highest point on the left half, or the left button if the highest point on the left half was higher or if both points were equally high. The next trial began 2.65 s after the participant's response. This study task was used to ensure that participants encoded each drawing in a perceptually detailed manner. After the filler picture, a rectangle was shown on the screen, and the participant was asked if the last picture was wider than the rectangle. This procedure was used in order to minimize the contribution of rehearsal on subsequent memory performance. Participants were then given feedback on their performance during the study run and allowed a moment to blink or stretch if necessary. The average delay between the last study picture and the test phase was ~1 min.

After each study phase, a cue was presented indicating that the test phase would be either a general test or a specific test. Participants were instructed that three types of pictures would be presented: pictures identical to those seen in the study phase (old/same), modified versions of studied pictures (old/different), and new pictures. In the general test, instructions were to endorse any version of a studied picture as "old" and to endorse previously unseen pictures as "new." In the specific test, instructions were to endorse pictures that were physically identical to ones that were studied as "old" and to endorse modified and previously unseen pictures as "new." Each test phase consisted of five identical old pictures, five modified old pictures, and five new pictures. Each picture was presented for 300 s and then replaced by a fixation cross. The next trial began 2.65 ms after the participant's response.

The specific and general study test blocks were presented in a pseudorandom order, with the provision that there were no more than two consecutive blocks of either test type. The mapping of pictures to tests (specific versus general) and stimulus type (old/same versus old/different versus new) was counterbalanced across participants. The hand associated with each response type ("old" and "new") was also counterbalanced, resulting in 12 different counterbalancing combinations, one for each participant.

### ERP Recording and Analysis

Electroencephalographic recordings were made from 21 tin electrodes imbedded in an elastic cap at standard scalp locations (Fpz, Fp1, Fp2, Fz, F3, F4, F7, F8, Cz, C3, C4, Pz, P3, P4, T3, T4, T5, T6, Oz, O1, O2). We refer to the three left and right frontal electrode pairs as anterior frontal (Fp1/Fp2), midfrontal (F3/F4), and lateral frontal (F7/F8). Horizontal and vertical eye movements were recorded with an electrode below the right eye and with electrodes lateral to each eye. The band-pass was 0.1–100 Hz. Online recordings were referenced to the left mastoid electrode, and the reference was changed to the average of the left and right mastoid recordings offline. Trials containing artifacts due to eye movements were excluded prior to averaging (mean = 12%, SEM = 3%). Statistical analyses were conducted using the 0.05 alpha level, with the Huynh-Feldt correction when appropriate.

Reported ERP analyses included all artifact-free trials, regardless of recognition accuracy. Given the small number of recognition errors, signal-to-noise ratios were insufficient for computing ERPs separately for incorrect trials. We felt that limiting ERP analyses to correct trials might have introduced additional differences between the tests, based on the following reasoning. We assume that recollection varies across trials in both test conditions and that correct responses on the specific test tend to require stronger recollection than on the general test. Excluding incorrect trials might thereby exaggerate the difference between conditions by excluding a greater proportion of weak-recollection trials on the specific test than on the general test. We repeated the statistical analyses reported in this study on ERPs from correct trials only, and as might be expected given the small number of errors, the pattern of results was the same.

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### References

Allan, K., and Rugg, M.D. (1997). An event-related potential study of explicit memory on tests of cued recall and recognition. Neuropsychologia *35*, 387–397.

Buckner, R.L. (1996). Beyond HERA: contributions of specific prefrontal areas to long-term memory retrieval. Psychon. Bull. Rev. *3*, 149–158.

Buckner, R.L., Koustaal, W., Schacter, D.L., Dale, A.M., Rotte, M., and Rosen, B.R. (1998a). Functional–anatomic study of episodic retrieval. II. Selective averaging of event-related fMRI trials to test the retrieval success hypothesis. Neuroimage *7*, 163–175.

Buckner, R.L., Koustaal, W., Schacter, D.L., Wagner, A.D., and Rosen, B. R. (1998b). Functional–anatomic study of episodic retrieval using fMRI. I. Retrieval effort versus retrieval success. Neuroimage *7*, 151–162.

Butters, M.A., Kaszniak, A.W., Glisky, E.L., Eslinger, P.J., and Schacter, D.L. (1994). Recency discrimination deficits in frontal patients. Neuropsychology *8*, 343–353.

Cohen, J.D., and Servan-Schreiber, D. (1992). Context, cortex, and dopamine: a connectionist approach to behavior and biology in schizophrenia. Psychol. Rev. *99*, 45–77.

Cohen, J.D., Braver, T.S., and O'Reilly, R.C. (1996). A computational approach to prefrontal cortex, cognitive control, and schizophrenia: recent developments and current challenges. Philos. Trans. R. Soc. Lond. B Biol. Sci. *351*, 1515–1527.

D'Esposito, M., Postle, B., Ballard, D., and Lease, J. (1999). Maintenance versus manipulation of information held in working memory: an event-related fMRI study. Cogn. Brain Res., in press.

Donaldson, D.I., and Rugg, M.D. (1998). Recognition memory for new associations: electrophysiological evidence for the role of recollection. Neuropsychologia *36*, 377–395.

Düzel, E., Yonelinas, A.P., Mangun, G.R., Heinze, H., and Tulving, E. (1997). Event-related brain potential correlates of two states of conscious awareness in memory. Proc. Natl. Acad. Sci. USA *94*, 5973–5978.

Fuster, J.M. (1989). The Prefrontal Cortex (New York: Raven Press).

Gershberg, F.B., and Shimamura, A.P. (1995). Impaired use of organizational strategies in free recall following frontal lobe damage. Neuropsychologia *13*, 1305–1333.

Goldman-Rakic, P.S. (1987). Circuitry of primate prefrontal cortex and regulation of behavior by representational memory. In Handbook of Physiology, Volume V, F. Plum, ed. (Bethesda, MD: American Physiological Society), pp. 373–417.

Hirst, W., and Volpe, B.T. (1988). Memory strategies with brain damage. Brain Cogn. *8*, 379–408.

Incisa della Rochetta, A., and Milner, B. (1993). Strategic search and retrieval initiation: the role of the frontal lobes. Neuropsychologia *31*, 503–524.

Janowsky, J.S., Shimamura, A.P., and Squire, L.R. (1989). Source memory impairment in patients with frontal lobe lesions. Neuropsychologia *27*, 1043–1056.

Jetter, W., Poser, U., Freeman, R.B., and Markowitsch, H.J. (1986). A verbal long-term memory deficit in frontal lobe damaged patients. Cortex *22*, 229–242.

Johnson, M.K., Hashtroudi, S., and Lindsay, D. (1993). Source monitoring. Psychol. Bull. *114*, 3–28.

Johnson, M.K., Kounios, J., and Nolde, S.F. (1996). Electrophysiological brain activity and memory source monitoring. Neuroreport *7*, 2929–2932. Erratum: Neuroreport *8*, 1317–1320.

Johnson, M.K., Nolde, S.F., Mather, M., Kounios, J., Schacter, D.L., and Curran, T. (1997). Test format can affect the similarity of brain activity associated with true and false recognition. Psychol. Sci. *8*, 250–257.

Johnson, R., Jr. (1995). Event-related potential insights into the neurobiology of memory systems. In Handbook of Neuropsychology, Volume 10, F. Boller and J. Grafman, eds. (Amsterdam: Elsevier), pp. 135–164.

Kapur, S., Craik, F.I.M., Jones, C., Brown, G.M., Houle, S., and Tulving, E. (1995). Functional role of the prefrontal cortex in memory retrieval: a PET study. Neuroreport *6*, 1880–1884.

Kazmerski, V., and Friedman, D. (1997). Old–new differences in direct and indirect memory tests using pictures and words in within- and cross-form conditions: event-related potential and behavioral measures. Cogn. Brain Res. *5*, 255–272.

Knight, R.T., and Grabowecky, M. (1995). Escape from linear time: prefrontal cortex and conscious experience. In The Cognitive Neurosciences, M.S. Gazzaniga, ed. (Cambridge, MA: MIT Press), pp. 1357–1371.

Kutas, M., and Dale, A.M. (1997). Electrical and magnetic readings of mental functions. In Cognitive Neuroscience, M.D. Rugg, ed. (Cambridge, MA: MIT Press), pp. 197–242.

Luria, A.R. (1973). The frontal lobes and regulation of behavior. In Psychophysiology of the Frontal Lobes, K.H. Pribram and A.R. Luria, eds. (New York: Academic Press), pp. 3–28.

Mangels, J.A. (1997). Strategic processing and memory for temporal order in patients with frontal lobe lesions. Neuropsychology *11*, 207–221.

Mark, R.E., and Rugg, M.D. (1998). Age effects on brain activity associated with episodic memory retrieval. Brain *121*, 861–873.

McAndrews, M.P., and Milner, B. (1991). The frontal cortex and memory for temporal order. Neuropsychologia *29*, 849–859.

McCarthy, G., and Wood, C.C. (1985). Scalp distributions of event-related potentials: an ambiguity associated with analysis of variance models. Electroencephalogr. Clin. Neurophysiol. *62*, 203–208.

Milner, B., Corsi, P., and Leonard, G. (1991). Frontal lobe contribution to recency judgements. Neuropsychologia *29*, 601–618.

Moscovitch, M. (1989). Confabulation and the frontal systems: strategic versus associative retrieval in neuropsychological theories of memory. In Varieties of Memory and Consciousness: Essays in Honor of Endel Tulving, H.L. Roediger III and F.I.M. Craik, eds. (Hillsdale, NJ: Erlbaum), pp. 133–160.

Nolde, S.F., Johnson, M.K., and Raye, C.L. (1998a). The role of the prefrontal cortex during tests of episodic memory. Trends Cogn. Sci. *2*, 399–406.

Nolde, S.F., Johnson, M.K., and D'Esposito, M. (1998b). Left prefrontal activation during episodic remembering: an event-related fMRI study. Neuroreport *9*, 3509–3514.

Nyberg, L., Tulving, E., Habib, R., Nilsson, L., Kapur, S., Houle, S., Cabeza, R., and McIntosh, A.R. (1995). Functional brain maps of retrieval mode and recovery of episodic information. Neuroreport *7*, 249–252.

Nyberg, L., Cabeza, R., and Tulving, E. (1996). PET studies of encoding and retrieval: the HERA model. Psychon. Bull. Rev. *3*, 135–148.

Paller, K.A. (1993). Elektrophysiologische Studien zum Menschlichen Gedächtnis [Electrophysiological studies of human memory]. Z. EEG EMG *24*, 24–33.

Paller, K.A., and Kutas, M. (1992). Brain potentials provide neurophysiological support for the distinction between conscious recollection and priming. J. Cogn. Neurosci. *4*, 375–391.

Paller, K.A., Kutas, M., and McIsaac, H. (1995). Monitoring conscious recollection via the electrical activity of the brain. Psychol. Sci. *6*, 107–111.

Paller, K.A., Bozic, V.S., Ranganath, C., Grabowecky, M., and Yamada, S. (1999). Brain waves following remembered faces index conscious recollection. Cogn. Brain Res. *7*, 519–531.

Petrides, M., Alivisatos, B., Evans, A.C., and Meyer, E. (1993). Dissociation of mid-dorsolateral from posterior dorsolateral frontal cortex in memory processing. Proc. Natl. Acad. Sci. USA *90*, 873–877.

Posner, M.I., and Raichle, M.E. (1995). Précis of Images of Mind. Behav. Brain Sci. *18*, 327–383.

Pribram, K.H. (1973). The primate prefrontal cortex—executive of the brain. In Psychophysiology of the Frontal Lobes, K.H. Pribram and A.R. Luria, eds. (New York: Academic Press), pp. 293–314.

Ranganath, C., and Paller, K.A. (1999). Frontal brain activity during episodic and semantic retrieval: insights from event-related potentials. J. Cogn. Neurosci., in press.

Roskies, A.L. (1994). Mapping memory with positron emission tomography [comment]. Proc. Natl. Acad. Sci. USA *91*, 1989–1991.

Rugg, M.D. (1995). ERP studies of memory. In Electrophysiology of Mind, M.D. Rugg and M.G.H. Coles, eds. (New York: Oxford University Press), pp. 132–170.

Rugg, M.D. (1998). Convergent approaches to electrophysiological and hemodynamic investigations of memory. Hum. Brain Mapp. *6*, 394–398.

Rugg, M.D., Fletcher, P.C., Frith, C.D., Frackowiak, R.S.J., and Dolan, R.J. (1996). Differential activation of the prefrontal cortex in successful and unsuccessful memory retrieval. Brain *119*, 2073–2083.

Rugg, M.D., Mark, R., Walla, P., Schloersheidt, A., Birch, C., and Allan, K. (1998). Dissociation of the neural correlates of implicit and explicit memory. Nature *392*, 595–598.

Schloerscheidt, A.M., and Rugg, M.D. (1997). Recognition memory for words and pictures: an event-related potential study. Neuroreport *8*, 3281–3285.

Senkfor, A., and Van Petten, C. (1998). Who said what: an event-related potential investigation of source and item memory. J. Exp. Psychol. Learn. Mem. Cogn. *4*, 1005–1025.

Shallice, T. (1982). Specific impairments in planning. Philos. Trans. R. Soc. Lond. B Biol. Sci. *298*, 199–209.

Shimamura, A.P. (1996). The role of the prefrontal cortex in monitoring and controlling memory processes. In Implicit Memory and Metacognition. L. Reder, ed. (Mahwah, NJ: Erlbaum), pp. 259–274.

Shimamura, A.P., Janowsky, J.S., and Squire, L.R. (1990). Memory for the temporal order of events in patients with frontal lobe lesions and amnesic patients. Neuropsychologia *28*, 803–813.

Smith, M.E. (1993). Neurophysiological manifestations of recollective experience during recognition memory judgments. J. Cogn. Neurosci. *5*, 1–13.

Snodgrass, J., and Vanderwort, M. (1980). A standardized set of 260 pictures: norms for name agreement, image agreement, familiarity, and visual complexity. J. Exp. Psychol. Learn. Mem. Cogn. *6*, 174–215.

Stuss, D.T., Alexander, M.P., Palumbo, C.L., Buckle, L., Sayer, L., and Pogue, J. (1994). Organizational strategies of patients with unilateral or bilateral frontal lobe injury in word list learning tasks. Neuropsychology *8*, 355–373.

Trott, C.T., Friedman, D., Ritter, W., and Fabiani, M. (1997). Item and source memory: differential age effects revealed by event-related brain potentials. Neuroreport *8*, 3373–3378.

Tulving, E. (1983). Elements of Episodic Memory (Oxford: Clarendon Press).

Tulving, E., Kapur, S., Craik, F.I.M., Moscovitch, M., and Houle, S. (1994). Hemispheric encoding/retrieval asymmetry in episodic memory. Proc. Natl. Acad. Sci. USA *91*, 2016–2020.

Wheeler, M., Stuss, D.T., and Tulving, E. (1995). Frontal lobe damage produces episodic memory impairment. J. Int. Neuropsychol. Soc. *1*, 525–536.

Wilding, E.L. (1999). Separating retrieval strategies from retrieval success: an event-related potential study of source memory. Neuropsychologia, in press.

Wilding, E.L., and Rugg, M.D. (1996). An event-related potential study of recognition memory with and without retrieval of source. Brain *119*, 889–905.

Wilding, E.L., and Rugg, M.D. (1997a). An event-related potential study of memory for words spoken aloud or heard. Neuropsychologia *35*, 1185–1195.

Wilding, E.L., and Rugg, M.D. (1997b). Event-related potentials and the recognition memory exclusion task. Neuropsychologia *35*, 119–128.

Wilding, E.L., Doyle, M., and Rugg, M.D. (1995). Recognition memory with and without retrieval of study context: an event-related potential study. Neuropsychologia *33*, 743–767.